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Feather Morphology In Biological Research

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The feather, because of its relative simplicity, its availability, and its response to different physiological conditions that can be regulated quantitatively, is a valuable instrument for studies in various biological problems. Since the brilliant studies of Lillie, et al. (1932,[1] 1938,[2] 1940,[3] 1940,[4] 1941,[5] 1943,[6] 1944[7]), the feather has received more and more attention. A review of the literature reveals that the feather is well adapted for studies in the physiology of development, experimental studies on pigmentation, various gonadic conditions, and analysis both of genetic and of endocrine factors. Feather follicles are responsive to certain endocrine differences when they exist, and transplants provide a means of analyzing endocrine and direct genetic effects in the development of feathers. Danforth and Foster[8] determined the relation between direct effects of genetic factors, and indirect effects of endocrine factors, in the production of individual differences. The authors found that in all cases investigated, the color and markings of feathers produced by the grafted skin were independent of peculiarities of the host, as long as both donor and host were of the same sex. However, the secondary sexual characteristics of feathers never became fixed, but were determined by the endocrine conditions that prevailed at the time a particular set of feathers was produced. Willier and Rawles[9] studied feather characterization in host-graft combinations between chick embryos of different breeds. Hamilton[10] studied the physiological properties of melanophores, and Ris,[11] the origin of melanophores in birds. The source of melanophores in regenerating feathers was studied by Foulks.[12] Eastlick and Wortham[13,14,15] studied the origin of subcutaneous melanophores and concluded that they, like the feather pigmenting chromatophores, were derived from the neural crest.

The feather is being used more and more as a valuable instrument for studies in various biological problems and because of the lack of uniformity in feather terminology appearing in literature, it seems advisable to describe and define the terms most frequently used, and to discuss the detailed characteristics typical of the flight feather of Gallus domesticus.

Nomenclature

When speaking of a feather or its structure, the terms dorsal and ventral are used with reference to the feather itself regardless of its location on the bird. Thus, the side of the feather that is usually exposed is considered dorsal and the opposite side ventral.

The term quill is generally used to include both rhachis (shaft) and calamus (Fig. 1A); the former term is applied to that portion of the quill distal to the distal umbilicus (Fig. 1A); the latter term, calamus, is applied to the hollow portion of the quill proximal to the distal umbilicus. The distal umbilicus is the pore at the distal end of the calamus located on

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the ventral side of the feather. The term proximal umbilicus (Fig. 1A) is applied to the pore at the end of the calamus.

The term hyporhachis (aftershaft) is applied to the afterfeather that emerges from the distal umbilicus on the ventral surface of the main feather (Fig. 1A). It may be vestigial or absent.

The term barb (ramus) is applied to the primary branch of the shaft (Fig. 1B). However, it is sometimes less commonly used to include the primary branch and its barbules.

The branches of the barb are termed barbules (Fig. 1B). Their structure is quite variable and often complex depending upon the location of the barbule, and the type of feather. They may be differentiated into proximal and distal barbules. The former are those on the side of the barb nearest the base of the feather; the term distal is applied to those on the opposite side of the barb.

The term hooklets (barbicels) is used by most authors to refer only to the strongly curved ventral hooked processes or outgrowths seen on the distal barbules. The term cilia refers to both dorsal and ventral out-gowths occurring on distal barbules.

The term vane or vexillum (Fig. 1A) refers to that part of a feather on one side of the shaft composed of barbs and generally of barbules. The term inner vane is applied to that vane which is overlapped superficially by the vane of the opposite side of the shaft of the contiguous feather.

The term plumules is applied to the small downy feathers; their extent and structure are variable.

Pennulus is a term introduced by Chandler[16] to designate the distal part of the barbule presenting the hooklets and cilia.

General Morphology

The quill of the flight-feather (Fig. 1A) is well developed, being differentiated into a fairly rigid shaft and a hollow calamus. The shaft's ventral surface presents a groove (Fig. 1A) which is usually quite pronounced in the region of the distal umbilicus gradually disappearing distally. The hyporhachis (after-feather) (Fig. 1A), although well developed in contour feathers, is practically absent in the flight and tail feathers being represented mainly by a few barbs.

The vanes of the flight feather are firm but often are unequal, the outer one usually being narrower. The barbs of the outer vane may be shorter and the angle of divergence from the rhachis may be less than that formed by the barbs of the inner vane. There is a great range in the degree of bilateral asymmetry, due to differences in growth-rate of the vanes. Chandler[16] states that the number of barbs per unit of measure follows a definite mathematical curve, and the number of barbules per unit of measure on the barbs follow a similar curve. The basal portion of the vane is downy in character.

The proximal and distal barbules of a typical flight feather present different characteristics. The distal barbules of both the inner and outer vanes present long hooklets and curved cilia (Fig. 1B). The proximal barbules present a series of cilia which sometimes resemble hooklets; however, one notes that only the distal barbules present the definitely curved hooked processes (hooklets). At 400 magnifications, tooth-like processes can be seen projecting from the ventral border of both the proximal and distal barbules, but should not be confused with true hooklets. Time has not permitted barb and barbule counts per unit of measure, although the writer believes a statistical "prediction" equation would be of value.

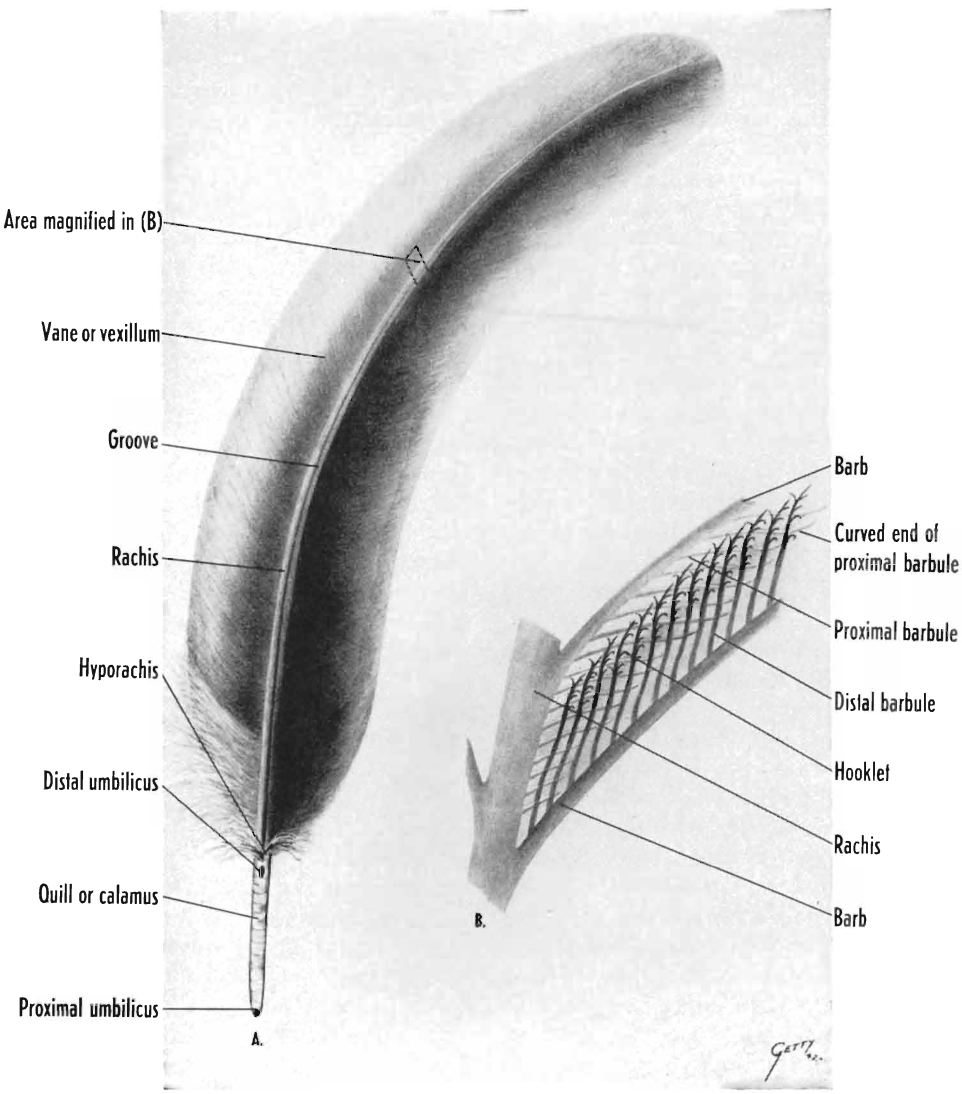
One notes that both the proximal and distal barbules are curved, giving the appearance of a longitudinal groove when examined under the microscope. This grooved or warped appearance is due to a twisting of the distal half or third of both the proximal and distal barbules, thus, the proximal halves of the barbules appear as flattened laminae whereas the pennulus or distal portions are twisted. The interlocking of the barbules is due to the distal barbules, which bear the hooklets, overlapping the scroll-like or twisted margin of the proximal barbules.

The elongated barbules frequently seen on the barbs at the basal (proximal end) of the vane of contour and wing feathers are downy in character. The long slender barbules of the down area of the vane present at intervals swollen, ring-like nodes. The base of the barbules in this area, however, is only slightly differentiated. The transition from the elongated barbules of the downy portion of the vane, to the differentiated distal and proximal barbules of the vane may, or may not be abrupt. The barbules of the body feathers differ mainly in simplification of structure.

Feather Growth and Regeneration

The order of formation of the shaft (rhachis) of the feather is strictly apicobasal and the order of age of the barbs is the same. Thus, the oldest part of the rhachis is at the tip of the feather and the oldest part of the barbs at the feather margin. Consequently, the order of age of the barbules is from margin to shaft along the barbs.

The experimental transplantations of Lillie and Wang[5] demonstrate that the



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general development of the feather is controlled by the papilla, which lies at the bottom of the feather follicles of the skin. Operations were performed on the papilla which remains behind at the bottom of the follicle when the feather is plucked or naturally dropped in the process of molting. The papilla, which Lillie and Wang believe is a persistent structure from the time of its embryonic origin, lies at the bottom of the feather follicle in the resting state after regeneration is complete.

The earlier work of Lillie and Juhn[2] indicated that the papilla was of composite origin, consisting of a dermal core and a thin covering of follicular epidermis, the so-called regeneration cells. The term regeneration cells is frequently used as equivalent to the epidermal component of the papilla. Wang[18] further analyzed the morphogenetic functions of the epidermal and dermal components of the papilla in feather regeneration, and concluded that the two components are mutually indispensable since neither can produce a feather alone. As both dermal and epidermis were involved in previous transplant experiments, Wang set out to delimit the morphogenetic functions of the epidermal and dermal components. A unique technique was devised by which the components of breast and saddle papillae could be separated and recombined. The epidermal coat of a papilla was destroyed, and the denuded dermal core transplanted into another follicle whose papilla had been previously completely removed. Local epidermis of the host tract grew over the transplant and thus a composite papilla was obtained. The resulting feather had a dermal portion coming from one tract, and the epidermal portion from the other. Some of the denuded dermal papillae were also rotated prior to implantation into empty follicles, in order to analyze the contribution of the separate components in the determination of feather orientation. Wang's data indicated that feathers from denuded papillae never exhibited the characteristics of the tract of origin (donor tract) but instead, exhibited the characteristics of the tract in which they were grown. He concluded, therefore, that tract specificity must be attributed to the epidermal (host tract) component of thet regenerating papilla. Wang, in another series of experiments, proved that an empty follicle will remain inactive except in the presence of a grafted papilla, intact or denuded, and thus demonstrated that the dermal component is indispensable for normal feather regeneration. Experiments in transplantation also demonstrated that the feather formed by the host tract epidermis owes its orientation and symmetry to an orienting influence of the dermal core. Wang believes that the influence of the dermal component is of a general nature, whereas the response of the follicular epidermis, in contrast, is very specific. The breast epidermis produced only breast feathers regardless of whether it was provided with the dermal papilla of its own, or of another tract; similarly, saddle epidermis produced only saddle feathers. Wang concluded that tract specificity e.g. growth rate, shape, form, structure and pigmentation is a function of the epidermal component of the papilla alone.

Wang also noted that feathers derived from untreated papillae retained the pigmentation of their original tract, regardless of the site of growth, but those from denuded papillae exchanged between breast and saddle took on the pigmentation of the host tract. The pigmentation followed the tract which contributed the epidermal component of the papilla. These findings are also in accord with observations that pigment cells are of neural-crest origin in both amphibians and birds (DuShane,[19] Eastlick,[20] Watterson,[21] Willier[22] and Rawles [23]).

Effects of Diet

The studies of Sanford[17] indicate that the actual structure of the chick feather is altered in birds fed various types of cereal grains and their by-products. The differences in structure, according to Sanford, appear to be due to differences in number of barbicels per unit area. Sanford's investigations involved the use of 6 experimental diets which resulted in plumages of different quality and structure. He observed that ground wheat and wheat shorts produced the greatest number of chicks with abnormal downy or silky plumage. Lack of uniformity of surface color and poor quality feathers also resulted when an oat groats diet was fed. Wheat bran and untreated oat hulls produced excellent feathering characterized by normal feather structure and pigmentation. However, autoclaved oat hulls resulted in poor feather quality characterized by lack of uniformity of plumage and color. Sanford concluded that those diets producing the most normal type feathers also produced feathers that have more barbicels per unit area than those produced by chicks receiving diets that produce abnormal appearing feathers.

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Losses in America's baby pig crop last spring were complicated by the appearance of a new type of virus disease.